Optimum size and number of seeds when seeds suffer pre-dispersal predation

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ABSTRACT

Question: What are the optimum size and number of seeds when plants suffer pre-dispersal seed predation?

Key assumptions of the model: There is a trade-off between the size and the number of seeds. A certain number of seeds is eaten at a certain stage of seed development from ovules to seeds. After seed predation, a plant may abort a certain number of uneaten seeds to concentrate its resources on the rest. Thus, the plant can adjust the size of its seeds by changing the numbers of seeds initially produced and flexibly aborted after seed predation.

Predictions: If the number of seeds eaten is unpredictable, surplus seeds are produced or not produced dependent on parameter values such as the resource cost of aborting uneaten seeds. When surplus seeds are produced, there is a limit to the number of seeds that develop successfully, and also seeds that develop successfully will be at least a certain minimum size. If the number of uneaten seeds is greater than the maximum number, the plant reduces these by aborting the number in excess of this limit and all seeds will attain the minimum size. All uneaten seeds develop without abortion if the number of uneaten seeds is smaller than the maximum number. When no surplus seed are produced, all uneaten seeds always develop without abortion irrespective of the number of seeds eaten. Plants are not likely to produce surplus seeds if only a small proportion of seeds is expected to be eaten or if each seed that does get eaten or aborted costs a large amount of resources.

Keywords: optimum seed number, optimum seed size, pre-dispersal predation, size–number trade-off, unpredictable predation.

INTRODUCTION

Pre-dispersal seed predation is widespread in plants and many studies have examined the effects of pre-dispersal seed predation on flower and fruit production (Crawley, 1992). In particular, the adaptive significance of surplus ovules (flowers) in relation to unpredictable loss of ovules or seeds has been studied theoretically (Kozlowski and Stearns, 1989; Ehrlén, 1991) and empirically (Hendrix, 1979, 1984; Louda, 1982; Marshall *et al.*, 1985; Garrish and Lee, 1989; Ehrlén, 1992, 1993, 1996;

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Guitian, 1993; Vaughton, 1993; Lowenberg, 1994; Guitian *et al.*, 1996; Medrano *et al.*, 2000; Gómez and Fuentes, 2001; Melser and Klinkhamer, 2001; Wise and Cummins, 2002; Wright and Meagher, 2003). Ehrlén (1991) developed a reserve-ovary model and showed that it is advantageous to produce surplus ovaries in environments where flower predation is unpredictable. Kozlowski and Stearns (1989) developed a model of bet-hedging and showed that it is advantageous to produce surplus zygotes so that the number of independent offspring can be flexibly adjusted in environments where the optimum brood size varies unpredictably among breeding attempts. Partial or full compensation of seeds (fruits) by overproduction of ovules (flowers) has been observed in many plants (Hendrix, 1979, 1984; Garrish and Lee, 1989; Guitian, 1993; Vaughton, 1993; Lowenberg, 1994; Traveset, 1994; Guitian *et al.*, 1996; Medrano *et al.*, 2000; Gómez and Fuentes, 2001; Melser and Klinkhamer, 2001; Wise and Cummins, 2002).

What, then, is the optimum seed size when plants suffer pre-dispersal predation of seeds at a certain stage of seed development? Since seed size, like seed number, is an important fitness component in responding to pre-dispersal predation of developing seeds, plants may flexibly adjust not only the number of independent seeds but also their size under a size–number trade-off of seeds. Nevertheless, most theoretical studies have focused only on flexible change in seed number, and have not paid attention to flexible change in seed size. When a fraction of developing seeds suffers predation, should a plant abort uneaten seeds to concentrate its limited resources on the remaining seeds to produce large seeds, or develop all seeds that are uneaten at the expense of seed size? If the latter is the case for low seed predation, surplus seeds do not exist in the sense that no seeds are aborted even if predation is low. Thus, to understand completely the seed production strategy in relation to pre-dispersal seed predation, it is necessary to examine both the optimum size and number of seeds assuming a size–number trade-off. However, no previous studies have done this. Although Smith and Fretwell (1974) analysed optimum offspring size assuming a size–number trade-off, this model did not consider the effects of pre-dispersal offspring predation on optimum offspring size.

In this article, assuming a size–number trade-off of seeds, we analyse the optimum size and number of seeds when plants suffer pre-dispersal predation of seeds at a certain stage of seed development. We develop two models. In the first, the frequency of predation does not vary spatially and plants can predict the frequency. This model is used to critically analyse the optimum number of seeds initially produced and the optimum seed size. In the second model, frequency varies and plants cannot predict the frequency. In this model, a plant may abort a certain number of uneaten seeds to concentrate its resources on the remaining seeds when seed predation is low. This model is used to critically analyse the optimum number of uneaten seeds aborted and the resulting seed size. Using these two models, we analyse the dependences of the optimum number of seeds initially produced, the optimum number of uneaten seeds aborted, and the optimum size of seeds on the mean and variance in the number of seeds eaten and the amount of resources lost per eaten seed.

SEED PRODUCTION WHEN FREQUENCY OF PREDATION DOES NOT VARY

We first analyse the optimum seed production when the frequency of predation does not vary spatially – that is, plants can predict the frequency. Under this condition, we need not consider abortion of uneaten seeds by plants because they can adjust exactly the number of seeds successfully developed by changing the number of seeds initially produced. We analyse two situations of predation attack on plants: a constant number of seeds is eaten irrespective of the number of seeds initially produced, and a given proportion of seeds

initially produced is eaten. The latter represents the situation in which larger plants producing many flowers (seeds) suffer higher seed predation (De Steven, 1983; Hainsworth *et al.*, 1984; Molau *et al.*, 1989; Ehrlén, 1991; Bullock *et al.*, 1994; Nakamura *et al.*, 1995; Brody and Mitchell, 1997; Ohashi and Yahara, 2000; Leimu *et al.*, 2002).

The model

Let R and N denote the amount of resources allocated to seed production by a plant and the number of seeds initially produced, respectively, of which x number of seeds is eaten and the remaining $N - x$ seeds develop successfully. The resources already allocated to the eaten seeds are lost. Predation occurs at the time when individual seeds have become size r (i.e. r resources are lost per seed eaten). $R \geq rN$ must be satisfied because rN resources are allocated to the seeds before predation. Seed size, S, is defined as follows:

$$S = \frac{R - rx}{N - x}. \tag{1}$$

The amount of resources allocated to the successfully developed seeds is $R - rx$ and is divided by the number of those seeds, $N - x$. We assume that the size–number trade-off of seeds is inversely linear, although it has been predicted to be inversely non-linear (Sakai and Harada, 2001a, 2001b; Sakai and Sakai, 2005). This simplification is admissible because the results do not change qualitatively even if an inversely non-linear trade-off is assumed. S becomes very large if x is nearly equal to N, although there would be an upper limit in seed size in actual organisms. However, this discrepancy does not affect the results, since the probability that one seed is successfully established will be saturated by an increase in S (see below). The fitness of a plant is the number of seeds successfully established in the next generation. Let $G(S)$ be the probability that one seed of size S is successfully established. G is a monotonically increasing sigmoid function that satisfies $G(0) = 0$, and the probability that one seed is successfully established saturates as S increases. We assume no density regulation at the stage of seedling establishment, although those seedlings may be later subject to density-dependent mortality, which does not depend on seed size. We assume the following for G in the numerical examples:

$$G(S) = \exp(-b/S), \tag{2}$$

where b is the optimum seed size in the model of Smith and Fretwell (1974). The fitness, ϕ, is

$$\phi = G(S)(N - x). \tag{3}$$

A constant number of seeds is eaten irrespective of the number of seeds initially produced

We here show the optimum seed production when a constant number of seeds is eaten irrespective of the number of seeds initially produced, N. In this situation, x does not depend on N, and the seed size is given by equation (1). Thus, the fitness can be rewritten as:

$$\phi = (R - rx)\frac{G(S)}{S}. \tag{4}$$

The optimum seed size, S_1^*, and the optimum number of seeds initially produced, N_1^*, are obtained as shown in Appendix 1. S_1^* is the same as that in the model of Smith and Fretwell

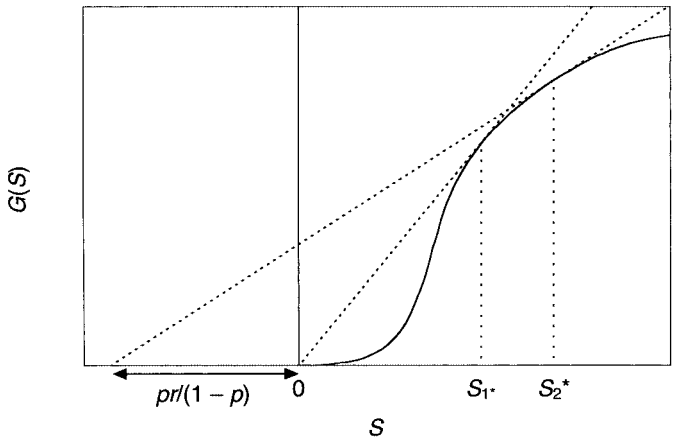

Fig. 1. The optimum seed sizes, S_1* and S_2*, for the situations in which a constant number of seeds is eaten irrespective of the number of seeds initially produced, and a given proportion of seeds initially produced is eaten, respectively. S_1* is at the point where $G'(S_1^*) = G(S_1^*)/S_1^*$ holds, and is the same solution as that in the model of Smith and Fretwell (1974). S_2* is at the point where $G'(S_2^*) = \dfrac{G(S_2^*)}{\dfrac{pr}{1-p} + S_2^*}$ holds, and is larger than S_1*.

(1974) (Fig. 1). S_1* is independent of the number of seeds eaten, x, the amount of resources lost per eaten seed, r, and the amount of resources allocated to seed production, R. N_1* increases with an increase in x (Fig. 2A) and decreases with an increase in r (Fig. 2B).

A given proportion of seeds initially produced is eaten

We next show the optimum seed production when a given proportion of seeds initially produced is eaten. Assume that a proportion p of seeds is eaten, i.e. $x = pN$. Then, the seed size and the fitness can be rewritten as:

$$S = \frac{R - prN}{(1-p)N}, \tag{5a}$$

$$\phi = G(S)(1-p)N = R\,\frac{G(S)}{\dfrac{pr}{1-p} + S}. \tag{5b}$$

The optimum seed size, S_2*, and the optimum number of seeds initially produced, N_2*, are obtained as shown in Appendix 2. S_2* is larger than that in the previous situation, S_1* (Fig. 1). In contrast to the previous situation, S_2* increases with an increase in the proportion of seeds eaten, p (Fig. 3A). Also, S_2* increases with an increase in the amount of resources lost per eaten seed, r (Fig. 3B). If p is great or if r is small, N_2* increases with an increase in p (Fig. 2C). However, if p is small or if r is great, N_2* decreases with an increase in p (Fig. 2C). N_2* decreases with an increase in r (Fig. 2D).

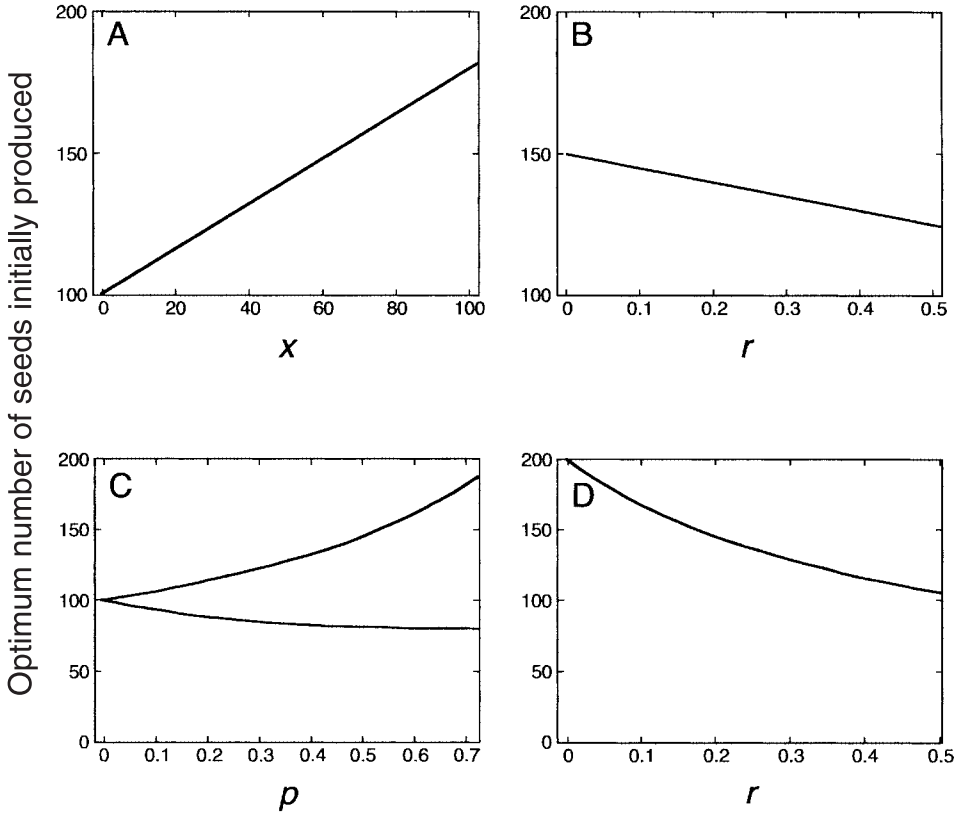

Fig. 2. The optimum number of seeds initially produced, N^*, dependent on the number of seeds eaten, x, the proportion of seeds eaten, p, and the amount of resources lost per seed eaten, r. A constant number of seeds is eaten irrespective of the number of seeds initially produced in (A) and (B), whereas a given proportion of seeds initially produced is eaten in (C) and (D). $b = 1$ and $R = 100$ in all panels. $r = 0.2$ in (A); $x = 50$ in (B); $r = 0.2$ in the upper line and $r = 0.9$ in the lower line in (C); $p = 0.5$ in (D).

SEED PRODUCTION WHEN FREQUENCY OF PREDATION VARIES

We next analyse the optimum seed production when the frequency of predation varies spatially – that is, plants cannot predict the frequency. We consider the abortion of uneaten seeds in these analyses so that plants can flexibly adjust the number of seeds successfully developed. We again analyse two situations, one in which a constant number of seeds is eaten irrespective of the number of seeds initially produced (but the number of seeds eaten varies spatially) and one in which a given proportion of seeds initially produced is eaten (but the fraction of seeds eaten varies spatially).

The model

As in the first model, N number of seeds is initially produced, of which x number of seeds is eaten during their development. Let $a(x)$ be the number of uneaten seeds aborted by

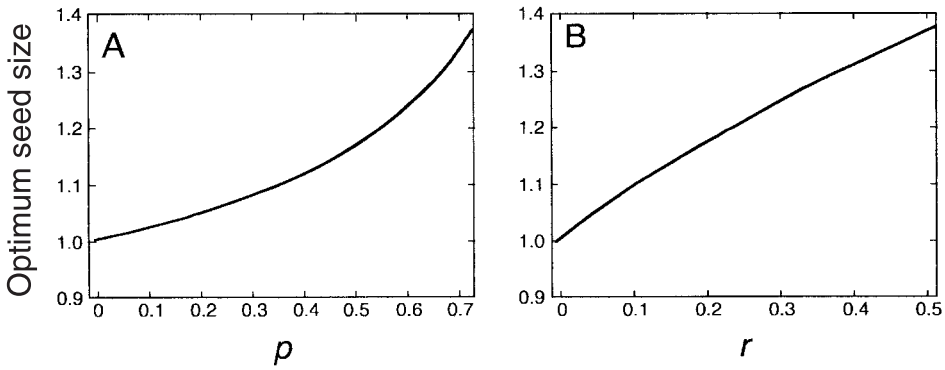

Fig. 3. The optimum seed size, S_2*, dependent on the proportion of seeds eaten, p, and the amount of resources lost per seed eaten, r. A given proportion of seeds initially produced is eaten in both (A) and (B). $b = 1$ and $R = 100$ in both panels. $r = 0.2$ in (A); $p = 0.5$ in (B).

a plant, where $a(x)$ may depend on x. The resources already allocated to eaten or aborted seeds are lost. For the sake of simplicity, we assume that the same amount of resources, r, is lost per seed eaten or aborted, assuming that abortion occurs immediately after seed predation. Thus, there remains an amount $R - rN$ of resources at the time when seed predation and abortion occur, since seeds are at size r at this time. The remaining $R - rN$ resources are divided by the remaining $N - x - a(x)$ number of seeds. Thus, seed size, S, is given by

$$S = r + \frac{R - rN}{N - x - a(x)}. \tag{6}$$

The fitness of a plant is assumed to be the arithmetic average over individuals in the same year. Let $f(x)$ be the probability that the number of seeds eaten is x. Then, the fitness is

$$\phi = \int_0^N G(S)[N - x - a(x)]f(x)dx = \int_0^N (R - rN)\frac{G(S)}{S - r}f(x)dx. \tag{7}$$

For situations in which a constant number of seeds is eaten and a given proportion of seeds is eaten, we assume the following gamma density distributions for f:

$$f(x) = \left(\frac{m}{v}\right)^{\frac{m^2}{v}} x^{\frac{m^2}{v}-1}\frac{\exp\left(-\frac{mx}{v}\right)}{\Gamma\left(\frac{m^2}{v}\right)}, \tag{8a}$$

and

$$f(x) = \left(\frac{m}{v}\right)^{\frac{m^2N}{v}} x^{\frac{m^2N}{v}-1}\frac{\exp\left(-\frac{mx}{v}\right)}{\Gamma\left(\frac{m^2N}{v}\right)}, \tag{8b}$$

respectively. In density distribution (8a), the mean and the variance in the number of seeds eaten, x, are given by m and v, whereas in density distribution (8b), they are given by mN and vN, respectively. The integration of $f(x)$ from $x = 0$ to N does not need to be equal to 1. If the integration, $\int_0^N f(x)dx$, is smaller than 1, it implies that all seeds are eaten at probability $1 - \int_0^N f(x)dx$ and a certain fraction of seeds survive at probability $\int_0^N f(x)dx$. We used gamma distributions because its L-shaped distribution form when the mean is small is likely for the frequency distribution of predation attack. Equation (2) is assumed for the probability of seed establishment, $G(S)$, in both situations.

The optimum number of seeds aborted and optimum seed size

We first show the optimum number of seeds aborted, $a^*(x)$, and the optimum seed size, S^*, dependent on the numbers of seeds initially produced, N, and eaten, x. In the following arguments, we need not consider the optimization of N or the shape of the density distribution for x since the arguments hold for given values of N and x. Also, the arguments hold for both types of predation frequency situations.

Fitness (7) implies that, for given values of N, x, and $f(x)$, the optimum $a^*(x)$ is the one that satisfies

$$\frac{G(S)}{S - r} \rightarrow \text{Max}, \tag{9}$$

noting that S depends on $a(x)$ but that the other parameters are independent of $a(x)$. This maximization is subject to the constraint $0 \leq a^*(x) \leq N - x$. It is both possible that uneaten seeds are aborted [i.e. $a^*(x) > 0$] when x is small and that they are never aborted irrespective of x [i.e. $a^*(x) = 0$ for all x]. In other words, surplus seeds are produced in the former, whereas they are not produced in the latter, in the sense that uneaten seeds are aborted when the frequency of predation is low.

Uneaten seeds are aborted when x *is small*

The condition that uneaten seeds are aborted when x is small is analysed in Appendix 3. There exists an optimum minimum seed size, S_m^* (Fig. 4); seeds smaller than this size are never produced. It is optimal to abort $a^*(x)$ number of uneaten seeds so that seed size (equation 6) becomes equal to S_m^*. S_m^* is smaller than the optimum seed size in the model of Smith and Fretwell (1974) (Fig. 4). S_m^* decreases with an increase in the amount of resources lost per eaten or aborted seed, r (see Appendix 3). However, S_m^* is independent of N and R; the same minimum size is the optimum irrespective of the number of seeds initially produced, N, and the amount of resources allocated to seed production, R.

When seeds with size S_m^* are produced, the number of seeds successfully developed is independent of x (see Appendix 3). In other words, there exists a maximum number of seeds developed, N_M^*; a plant aborts $a^*(x)$ uneaten seeds to produce seeds with the optimum maximum number, N_M^*, and the optimum minimum size, S_m^*, if the number of uneaten seeds, $N - x$, is greater than N_M^* (Fig. 5).

If the number of uneaten seeds, $N - x$, is smaller than N_M^*, no seed should be aborted [$a^*(x) = 0$] (Fig. 5). In this region, the size and the number of seeds developed increases and decreases, respectively, with an increase in x.

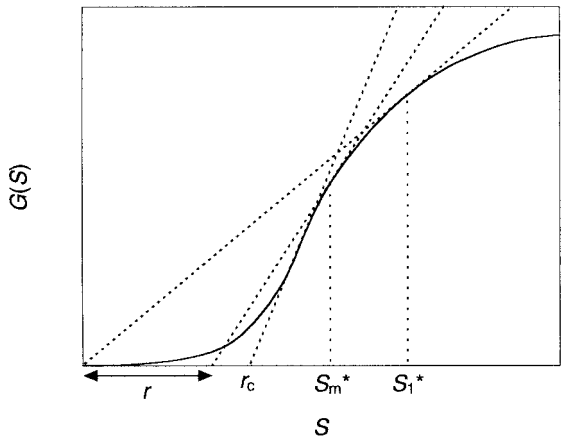

Fig. 4. The optimum minimum seed size, S_m*, and the optimum seed size, S_1*, in the model of Smith and Fretwell (1974). S_m* is at the point where $G'(S_m^*) = G(S_m^*)/(S_m^* - r)$ holds, which is smaller than S_1*. r_c represents the critical value of r, the point where the horizontal axis crosses the tangent from the inflection point of $G(S)$. If $r \geq r_c$, S_m* that satisfies condition (13a) does not exist. Also, S_m* cannot be realized if it is smaller than the minimum seed size possibly realized when no seeds are eaten or aborted, R/N.

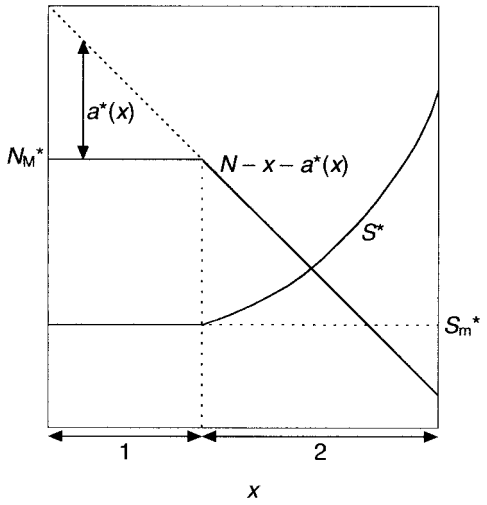

Fig. 5. The number of seeds successfully developed, $N - x - a^*(x)$, and the optimum seed size, S*, dependent on the number of seeds eaten, x. In region 1, uneaten seeds are aborted [$a^*(x) > 0$] so that seeds with the optimum minimum size, S_m*, and the optimum maximum number, N_m*, are produced irrespective of x. In region 2, no uneaten seeds are aborted [$a^*(x) = 0$] and the size and the number of seeds successfully developed are $r + (R - rN)/(N - x)$ and $N - x$, respectively.

Uneaten seeds are never aborted irrespective of x

Uneaten seeds are never aborted irrespective of x if the optimum minimum seed size, S_m*, is never realized with any values of x and $a(x)$. This occurs if S_m* does not exist (i.e. if r is larger than r_c in Fig. 4), or if S_m* exists but is never realized (i.e. the minimum seed size

possibly realized when no seeds are eaten or aborted, R/N, is greater than S_m^*) (see Appendix 4). In these cases, a plant always develops all uneaten seeds without abortion. The size and the number of seeds developed increases and decreases, respectively, with an increase in the number of seeds eaten, x, for the whole region of x, as in region 2 in Fig. 5.

The optimum number of seeds initially produced and size of seeds developed

We next show the optimum number of seeds initially produced, N^*, and the maximum number of seeds developed, N_M^*, numerically obtained for the situations in which a constant number of seeds is eaten and a given proportion of seeds is eaten [gamma density distribution (8a) and (8b) are assumed for $f(x)$, respectively]. We also show the seed size when the number of seeds eaten is equal to the mean [$x = m$ and $x = mN$ in density distributions (8a) and (8b), respectively] to illustrate characteristic changes in seed size.

A constant number of seeds is eaten irrespective of the number of seeds initially produced

N^* increases with an increase in the mean number of seeds eaten, m, in density distribution (8a) (Fig. 6A). N_M^* (and S_m^*) exists if m is great (uneaten seeds are aborted if the number of uneaten seeds is greater than N_M^*), whereas N_M^* does not exist if m is small (all uneaten seeds always develop without abortion). N^* decreases with an increase in the amount of resources lost per seed eaten or aborted, r (Fig. 6B). N_M^* exists if r is small, whereas it does not exist if r is great. The seed size when $x = m$ is almost entirely independent of m and r (Figs. 7A and 7B). Thus, all these results are consistent with the (in)dependency of the optimum number of seeds initially produced, N_1^*, and the optimum seed size, S_1^*, in the model in which predation frequency does not vary spatially and a constant number of seeds is eaten irrespective of the number of seeds initially produced.

A given proportion of seeds is eaten

N^* increases with an increase in the positive constant m in the mean number of seeds eaten, mN, in density distribution (8b) if m is great or if r is small (Fig. 6C). N_M^* exists if m is great, whereas N_M^* does not exist if m is small. However, if m is small and if r is great, N^* decreases with an increase in m, and N_M^* does not exist (Fig. 6E). N^* decreases with an increase in r (Fig. 6D), and N_M^* exists if r is small, whereas it does not exist if r is great. The seed size when $x = mN$ increases with an increase in m or r for almost the entire region of each parameter (Figs. 7C and 7D). Thus, all these results are also consistent with the dependency of N_2^* and S_2^* in the model in which predation frequency does not vary spatially and a given proportion of seeds is eaten.

Effects of variance

Finally, we show the dependence of N^* on the variance for both situations of predation attack. N^* increases or decreases with an increase in the variance of the number of seeds eaten, v, in density distribution (8a) or in the positive constant v in the variance, vN, of density distribution (8b) (Figs. 8A–D). The former is likely if the amount of resources allocated to seed production, R, is great or if r is small, whereas the latter is likely if R is small or if r is great.

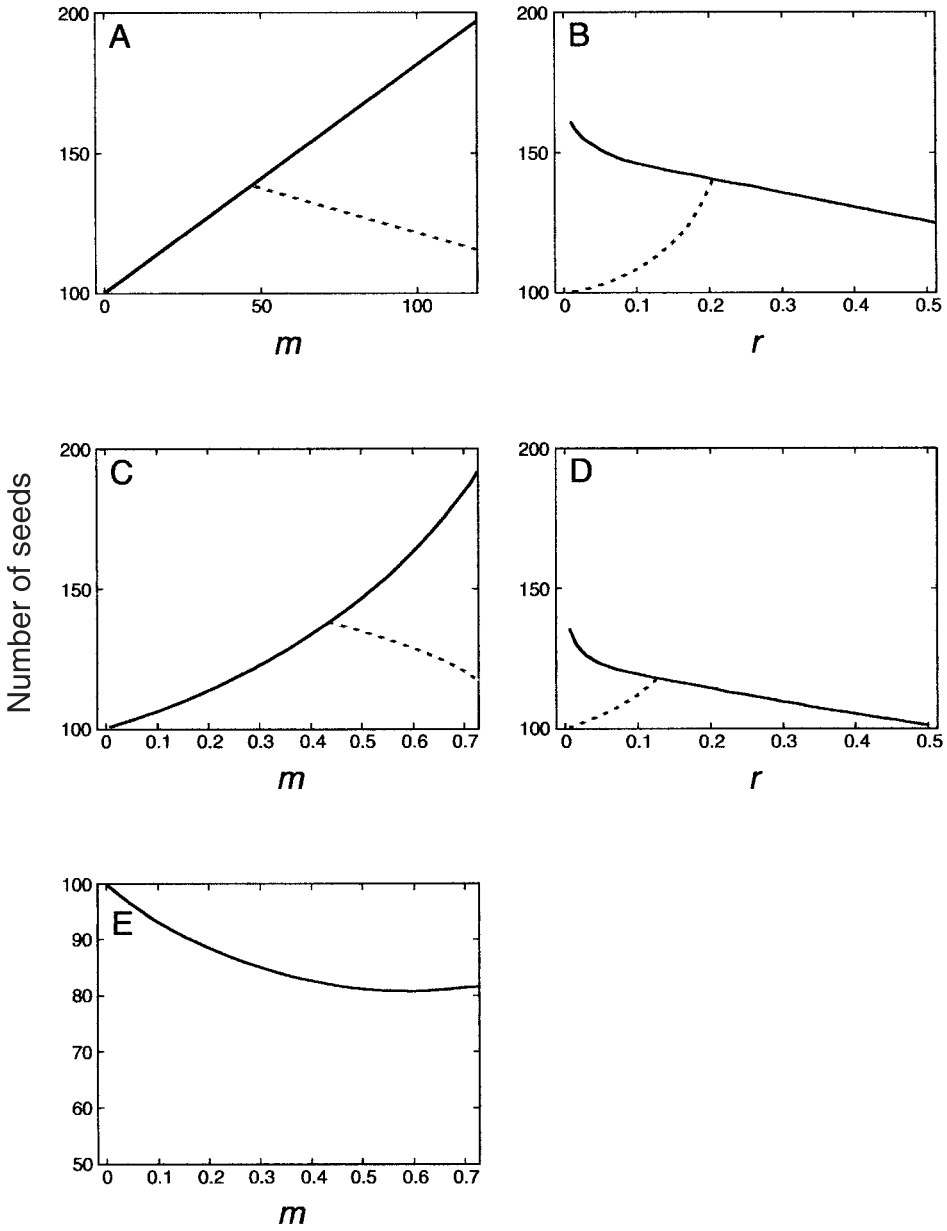

Fig. 6. The optimum number of seeds initially produced, N^* (solid lines), and the optimum maximum number of seeds developed, N_M^* (broken lines), dependent on the mean number of seeds eaten, m, the constant m in the mean number of seeds eaten, mN, and the amount of resources lost per seed eaten or aborted, r. A constant number of seeds is eaten irrespective of the number of seeds initially produced in (A) and (B) [density distribution (11a) is assumed], whereas a given proportion of seeds initially produced is eaten in (C–E) [density distribution (11b) is assumed]. N_M^* does not exist in the regions where broken lines do not appear. $b = 1$ and $R = 100$ in all panels. $r = 0.2$ and $v = 100$ in (A); $m = 50$ and $v = 100$ in (B); $r = 0.2$ and $v = 0.5$ in (C); $m = 0.2$ and $v = 0.5$ in (D); $r = 0.9$ and $v = 0.5$ in (E).

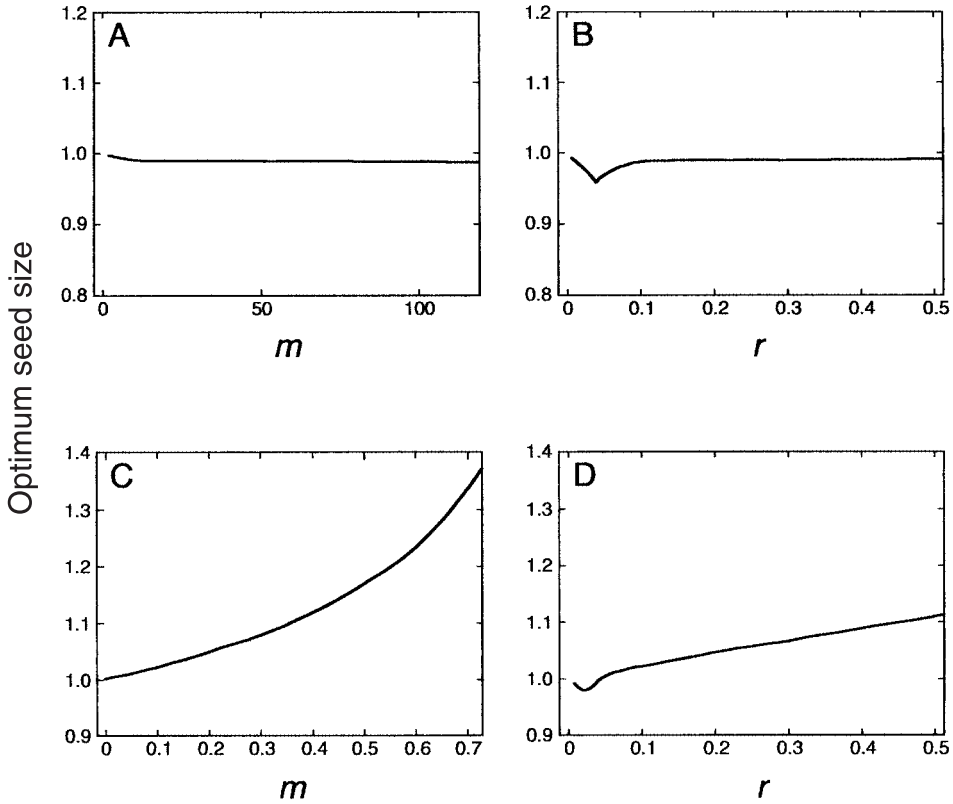

Fig. 7. The seed size when the number of seeds eaten is equal to the mean [$x = m$ and $x = mN$ in density distribution (11a) and (11b), respectively] dependent on the mean number of seeds eaten, m, the constant m in the mean number of seeds eaten, mN, and the amount of resources lost per seed eaten or aborted, r. A constant number of seeds is eaten irrespective of the number of seeds initially produced in (A) and (B) [density distribution (11a) is assumed], whereas a given proportion of seeds initially produced is eaten in (C) and (D) [density distribution (11b) is assumed]. $b = 1$ and $R = 100$ in all panels. $r = 0.2$ and $v = 100$ in (A); $m = 50$ and $v = 100$ in (B); $r = 0.2$ and $v = 0.5$ in (C); $m = 0.2$ and $v = 0.5$ in (D).

DISCUSSION

Optimum number of seeds initially produced and optimum seed size

The first model showed, and the second model confirmed, that the optimum number of seeds initially produced, N_1^* or N_2^*, and the optimum seed size, S_1^* or S_2^*, depend on parameter values somewhat differently between the cases in which a constant number of seeds is eaten irrespective of the number of seeds initially produced, N, and a given proportion of seeds initially produced is eaten.

In the former situation, plants can escape predation damage by producing many seeds initially because the number of uneaten seeds, $N - x$, increases with an increase in N without the cost of wasted resources due to predation. Hence, N_1^* increases with an increase in the number of seeds eaten, x (Fig. 2A).

In contrast, in the latter situation, an increase in the number of successfully developed seeds incurs a cost; i.e. $pr/(1-p)$ (= the total amount of resources lost due to predation/ the number of seeds successfully developed) represents the cost of losing resources per successful seed. Hence, N_2* decreases with an increase in the proportion of seeds eaten, p, if r is great because the cost is large, although N_2* increases if p becomes great (this is to avoid a very small brood size; not shown) (Fig. 2C). On the other hand, N_2* increases with an increase in p if r is small because the cost is small (Fig. 2C).

In both situations, N_1*(N_2*) decreases with an increase in the amount of resources lost per seed eaten, r (Figs. 2B and 2D). This is because the amount of resources actually allocated to the successfully developed seeds ($R - rN$ or $R - prN$) is less if r is greater, since r amount of resources is lost per seed eaten. Thus, because of this resource deficiency, predations that occur later during seed development (in which r would be great) should select for a decrease in the number of seeds initially produced.

The optimum seed size is independent of x and r when a constant number of seeds is eaten irrespective of the number of seeds initially produced, N, whereas it increases with an increase in p or r when a given proportion of seeds initially produced is eaten. This is because, in the size–number trade-off in the latter situation (equation 6a), an increase in N_1* causes a loss of pr resources due to predation. Because of this cost of increasing N, it is advantageous to increase S_2* with an increase in p or r rather than to change only N while keeping S_2* constant. In *Brassica rapa*, seed size is large in a population in which the seed predation rate is great (Nakamura *et al.*, 1995). In this population, a greater proportion of the fruits of larger plants is damaged (Nakamura *et al.*, 1995), and hence predation attack is similar to the latter rather than the former situation in our model. Thus, this report is consistent with our prediction.

In many plants, it is reported that larger plants producing many flowers (seeds) suffer higher seed predation (De Steven, 1983; Hainsworth *et al.*, 1984; Molau *et al.*, 1989; Ehrlén, 1991; Bullock *et al.*, 1994; Traveset, 1994; Nakamura *et al.*, 1995; Brody and Mitchell, 1997; Ohashi and Yahara, 2000; Leimu *et al.*, 2002). Hence, the latter situation may be more realistic for many plants.

In the present models, we assumed that r is independent of N_1*(N_2*). However, it is possible that r decreases with an increase in N_1*(N_2*) because the size of developing seeds at the stage of predation may be small if N_1*(N_2*) is great. Also, we assumed that plants cannot recover resources from aborted seeds. However, it is possible that a certain fraction of resources is recovered, and if this is the case, the cost of losing resources becomes small. Further analyses are necessary to examine the optimum seed production for these cases.

Compensation by surplus seeds

The second model shows that surplus seeds may or may not be produced; uneaten seed abortion can occur in the former, whereas it never occurs in the latter. Thus, the strategy of producing surplus seeds and aborting some of them is not always advantageous, even if plants suffer unpredictable pre-dispersal seed predation.

When surplus seeds are produced, there is an optimum minimum size, S_m*, and an optimum maximum number of seeds that develops, N_M* (Figs. 4 and 5). By aborting uneaten seeds, N_M* number of seeds with S_m* size is produced in the case that the number of uneaten seeds is greater than N_M*. Thus, plants should not develop all uneaten seeds by decreasing seed size even if the resources that had been allocated to the aborted seeds are

lost. Moreover, in this case, the same size and the same number of seeds are produced irrespective of the number of uneaten seeds. Thus, it can be assumed that seed production is fully compensated in terms of both size and number. The difference of N_M* from the number of seeds initially produced is the number of surplus seeds. On the other hand, all uneaten seeds develop without abortion if the number of uneaten seeds is smaller than N_M*. Seed production is only partially compensated since plants cannot produce N_M* number of seeds. The size of seeds increases with a decrease in the number of seeds developed as a result of the size–number trade-off.

Only a few experimental studies have simultaneously examined the response of seed size and number to different levels of predation or artificial flower removal. In *Cassia fasciculata*, removal of up to four of every five inflorescences resulted in nearly full compensation in fruit and seed production by the remaining, intact reproductive nodes (Garrish and Lee, 1989). The removal treatment did not change individual seed mass (Garrish and Lee, 1989). In *Helianthus annuus*, 15–30% removal of inflorescences also resulted in full compensation in seed number and size, although seeds were compensated not only by increases in the number of seeds produced per inflorescence but also by additional production of inflorescences (Pilson and Decker, 2002). In *Lathyrus vernus*, removal of flowers resulted in partial compensation in the number of seeds produced, and mean seed mass increased with a decrease in seed number (Ehrlén, 1992). These results are consistent with the above prediction. In *Sanicula arctopoides*, removal of umbels, both naturally by deer and by artificial clipping early in the flowering season, led to no loss of seed number, but there were thresholds both in timing and severity of removal beyond which plants were unable to compensate fully (Lowenberg, 1994). Lee and Bazzaz (1982) also reported similar results for *Cassia fasciculata*. However, neither Lowenberg nor Lee and Bazzaz examined the change in seed size. To test the present model, change in seed size as well as change in seed number should be examined in future studies.

On the other hand, surplus seeds are not produced, and all uneaten seeds always develop without abortion, if a small number of seeds is expected to be eaten (i.e. if m is small; Figs. 6A and 6C) or if a great amount of resources is lost per eaten or aborted seed (i.e. if r is great; Figs. 6B and 6D). In both conditions, the number of seeds initially produced is small since surplus seeds are not as necessary (m is small) or the cost of surplus seeds (the amount of resources lost per eaten or aborted seed) is large (r is great). Hence, it is advantageous to develop seeds that are all uneaten rather than to abort a few seeds, since individual seed size does not decrease greatly. Thus, the present model can explain the evolution of plants in which uneaten seed abortion is not observed. In fact, Andersson (1993) and Brody and Mitchell (1997) reported no compensation of seeds. Further studies are necessary to examine whether the proposed mechanisms in the present model are applicable to these species.

Non-production of surplus seeds can be advantageous because a size–number trade-off of seeds is assumed in the present model, in contrast to the previous models (Kozlowski and Stearns, 1989; Ehrlén, 1991) in which the cost of producing one seed is fixed. That is, our assumption allows flexible adjustment not only in seed number but also in seed size, and hence plants can develop all seeds that are uneaten by decreasing the size of individual seeds. The abortion of uneaten seeds occurs only if it is disadvantageous to decrease seed size. Thus, the size–number trade-off could have significant effects on the evolution of surplus seeds.

Effects of the variance in the number of seeds eaten

The optimum number of seeds initially produced, N^*, either increases or decreases with an increase in the variance in the number of seeds eaten (Fig. 8). Thus, counter-intuitively, it is possible that N^* is less in environments where seed predation is more unpredictable (i.e. the variance is larger). Sakai (1996, 1997) previously examined over-production of ovules (flowers) as an evolutionary strategy in environments where either pollinator or resource availability is unpredictable. Those studies showed that large variance in pollinator or resource availability selects for either an increase or a decrease in the number of ovules (flowers) produced by a plant. Hence, it could be concluded that unpredictable factors (pollination, resource availability, predation) do not always select for an increase in the number of surplus seeds, but rather they could select for its decrease.

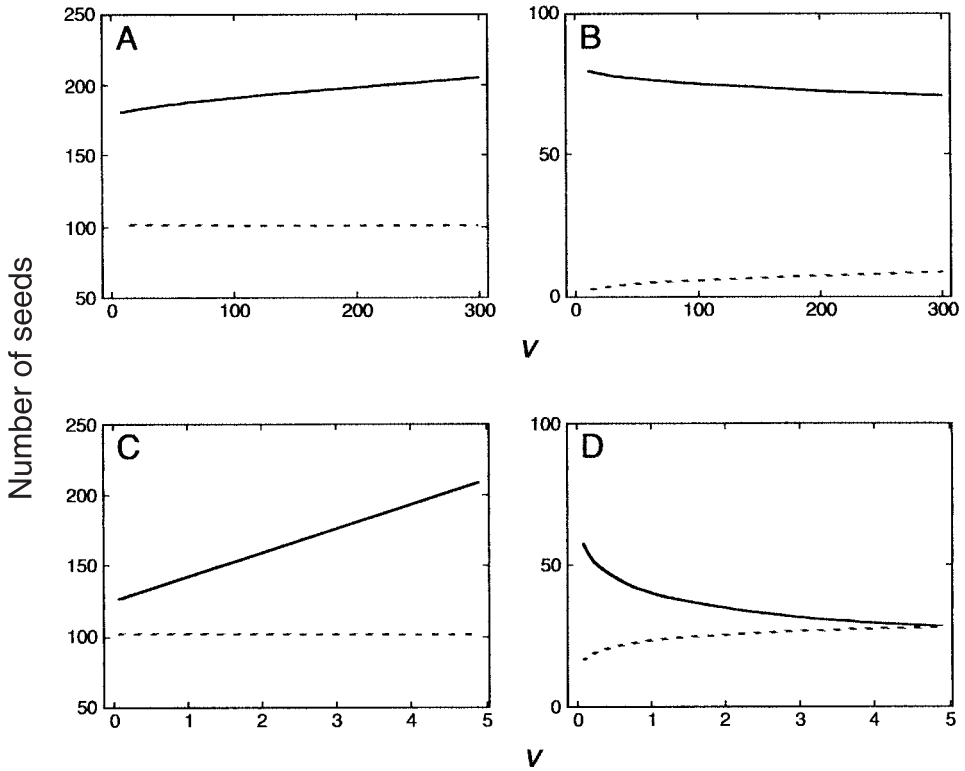

Fig. 8. The optimum number of seeds initially produced, N^* (solid lines), and the optimum maximum number of seeds developed, N_M^* (broken lines), dependent on the variance of the number of seeds eaten, v, and the constant v in the variance of the number of seeds eaten, vN. A constant number of seeds is eaten irrespective of the number of seeds initially produced in (A) and (B) [density distribution (11a) is assumed], whereas a given proportion of seeds initially produced is eaten in (C) and (D) [density distribution (11b) is assumed]. $b = 1$ in all panels. $m = 80$, $r = 0.2$, and $R = 100$ in (A); $m = 80$, $r = 0.24$, and $R = 100$ in (B); $m = 0.2$, $r = 0.01$, and $R = 100$ in (C); $m = 1$, $r = 0.2$, and $R = 20$ in (D).

Test of the present models

In tests of the predictions of the present models, plastic and evolutionary responses should be distinguished: the abortion of uneaten seeds in response to the degree of predation is an example of the former, whereas the number of seeds initially produced dependent on the frequency of predation, p or m, and the amount of resources lost per eaten or aborted seed, r, are examples of the latter. In the former tests (plastic response), artificial flower removal is useful. Here, flower removal should be conducted for as many levels as possible to detect the changes in the size and number of seeds developed, as in Fig. 5. On the other hand, in the latter tests (evolutionary response), population comparisons should be suitable using populations among which the values of p and r differ. This is because plants would have responded to the values of p and r over the evolutionary time scale. For example, p and r might change with elevation. Thus, tests on the number of seeds initially produced should be conducted for populations with certain values of p and r for many generations. However, experimental tests in which the values of p and r are artificially changed would also be useful to examine the resulting selection gradients for the tests of evolutionary responses.

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APPENDIX 1: A CONSTANT NUMBER OF SEEDS IS EATEN IRRESPECTIVE OF THE NUMBER OF SEEDS INITIALLY PRODUCED

The optimum seed size, S_1*, that maximizes fitness (4) in the text is given by S that maximizes $G(S)/S$, i.e.

$$G'(S_1^*) = G(S_1^*)/S_1^*, \tag{A1}$$

the same solution as that in the model of Smith and Fretwell (1974) (Fig. 1). The optimum number of seeds initially produced, N_1*, is given by

$$N_1^* = \frac{R + (S_1^* - r)x}{S_1^*}. \tag{A2}$$

APPENDIX 2: A GIVEN PROPORTION OF THE NUMBER OF SEEDS INITIALLY PRODUCED IS EATEN

The optimum seed size, S_2*, that maximizes fitness (5b) in the text is given by S that maximizes $G(S)/[pr/(1-p) + S]$; i.e. from the optimal conditions $d\phi/dS = 0$ and $d^2\phi/dS^2 < 0$, we have

$$G'(S_2^*) = \frac{G(S_2^*)}{\dfrac{pr}{1-p} + S_2^*}, \tag{A3}$$

$$N_2^* = \frac{R}{pr + (1-p)S_2^*}, \tag{A4}$$

and $G''(S_2^*) < 0$ must hold. By differentiating both sizes of these solutions with respect to p and r,

$$\frac{dS_2^*}{dp} = -\frac{rG(S_2^*)}{\{pr + (1-p)S_2^*\}^2\, G''(S_2^*)} > 0, \tag{A4a}$$

$$\frac{dS_2^*}{dr} = -\frac{(1-p)G(S_2^*)}{\{pr + (1-p)S_2^*\}^2\, G''(S_2^*)} > 0, \tag{A4b}$$

$$\frac{dN_2^*}{dp} = \frac{R\left[S_2^* - r + \dfrac{(1-p)rG(S_2^*)}{\{pr + (1-p)S_2^*\}^2\, G''(S_2^*)}\right]}{\{pr + (1-p)S_2^*\}^2}, \tag{A4c}$$

$$\frac{dN_2^*}{dr} = \frac{pR[(1-p)^2\, G(S_2^*) - \{pr + (1-p)S_2^*\}^2\, G''(S_2^*)]}{\{pr + (1-p)S_2^*\}^4\, G''(S_2^*)} < 0\,. \tag{A4d}$$

The signs of equations (A4a), (A4b), and (A4d) can be determined from the condition that $G''(S_2^*) < 0$. If p is great or if r is small, $dN_2^*/dp > 0$ is likely, whereas if p is small and if r is great, $dN_2^*/dp < 0$ is likely.

APPENDIX 3: UNEATEN SEEDS ARE ABORTED WHEN *x* IS SMALL

If

$$G'(S_m^*) = \frac{G(S_m^*)}{S_m^* - r} \tag{A5a}$$

is realized in the region where

$$S_m^* > r + \frac{R - rN}{N - x}, \tag{A5b}$$

S_m^*, which is derived from the optimal condition $d[G(S)/(S-r)]/dS = 0$, satisfies condition (9) in the text (also see Fig. 4). Condition (A5b) is necessary to make $a^*(x) > 0$. We refer to S_m^* as the optimum minimum seed size since it is disadvantageous to produce seeds smaller than this size. The dependence of S_m^* on r is obtained by differentiating both sides of solution (A5a) with respect to r:

$$\frac{dS_m^*}{dr} = \frac{G(S_m^*)}{(S_m^* - r)^2\, G''(S_m^*)} < 0\,. \tag{A6}$$

This is negative because $G''(S_m^*) < 0$ must hold so that S_m^* satisfies condition (9).

When seeds with size S_m^* are produced, the number of seeds successfully developed, $N - x - a^*(x)$, is independent of x:

$$N - x - a^*(x) = \frac{R - rN}{S_m^* - r}. \tag{A7}$$

This implies that the maximum number of seeds developed, N_M^*, exists; a plant aborts $a^*(x)$ uneaten seeds so that $N_M^* = N - x - a^*(x)$ holds, if the number of uneaten seeds, $N - x$, is greater than N_M^*.

If condition (A5b) is not satisfied but S_m^* satisfying condition (A5a) exists, S_m^* cannot be realized even if $a(x) = 0$. In this case, $G(S)/(S-r)$ decreases monotonously with an increase in S [i.e. with an increase in $a(x)$] since G is assumed to be a sigmoid function of S. Hence, no seeds should be aborted [$a^*(x) = 0$] and the optimal seed size is

$$S^* = r + \frac{R - rN}{N - x}. \tag{A8}$$

APPENDIX 4: UNEATEN SEEDS ARE NEVER ABORTED IRRESPECTIVE OF *x*

Uneaten seeds are never aborted irrespective of x if condition (A5) cannot be realized with any values of x and $a(x)$. This occurs if either of the following two conditions are satisfied.

First, r is large so that S_m* satisfying condition (A5a) does not exist; r is larger than or equal to the point (r_c in Fig. 4) where the horizontal axis and the tangent from the inflection point of $G(S)$ cross. Second, although r is smaller than r_c so that such S_m* exists, condition (A5b) is not satisfied even with $x = 0$; i.e. if

$$S_m^* \leq \frac{R}{N}. \tag{A9}$$

Under both conditions, $G(S)/(S - r)$ decreases monotonously with an increase in S irrespective of x, and hence $a^*(x) = 0$ for all x. The optimum seed size is given by equation (A8).